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WATER RETRIEVAL BY NORWAY RATS: BEHAVIOR AS DEDUCTION

R. J. Wallace

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ABSTRACT: The origin of behavior consistent with effective ("optimal") policies is an important topic in behavioral biology. In many cases, novel behavior patterns that emerge in unfamiliar situations are based on "trial and error" learning guided by rewards and punishments. The present work shows how an appropriate novel response can emerge full-blown in response to new contingencies if the situation has generic features that can be recognized. This work is concerned with object retrieval, i.e., carriage of valued objects to a place of safety by Norway rats (*Rattus norvegicus* (Berkenhout); Rodentia: Muridae). Experiment 1 shows that selective retrieval of objects containing water over dry objects of the same material can occur immediately when rats are made thirsty; it is unlikely that this is a specific adaptation, since the opportunity to retrieve water in this way would rarely arise under natural conditions. Experiment 2 shows that without initial exposure to both objects under *ad lib* conditions (where the retrieval preference was for the dry objects), a process of trial and error is apparent as thirsty rats learn to select the appropriate object. It is argued that if object retrieval behavior is linked to a generic incentive feature and features such as wetness are recoded into this general term, then appropriate object retrieval can be generated by a kind of deductive process. This type of generalist strategy would appear to be highly adaptive, in part because the usual tradeoffs between specialist and generalist strategies may not apply.

INTRODUCTION

According to behavioral optimization theory, much behavior consists of procedures for implementing policies that optimize quantities critical to Darwinian fitness. This formulation leaves open the means by which an animal comes to act in accordance with an optimal policy. For higher organisms, the procedures need not be pre-programmed; instead these animals can learn to respond in a manner that approaches optimality through feedback in the form of rewards and punishments. Learning of this sort often involves a degree of blind

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search, as reflected in the term "trial and error" (*cf.* the careful early descriptions of instrumental learning in Thorndike [1898] and Small [1900]). This would seem necessary insofar as the animal is dealing with aspects of the environment that are uncertain (*cf.* Plotkin & Odling-Smee, 1979; Johnston, 1982; Shettleworth, 1984).

On the other hand, if the defining features of a common situation can be recognized, it may be possible to generate new procedures by a kind of deductive process. In this case, recognizing a new situation in terms of its generic features may allow a novel but appropriate behavior pattern to emerge at the first opportunity. Possible examples of this are found in the object retrieval behavior of Norway rats and other rodents.

In its general form, this behavior is relatively straightforward. The animal leaves a place of safety and, on encounter with an object of some value which is also transportable, it carries the object back to the safe spot before 'consuming' it. This includes the case in which the animal has already discovered objects in a particular location and directs its activities, including the approach to the objects, toward carrying them to safety. In this case, the rodent appears to implement a policy that involves both maximizing consumption (either at present or at a later time) and minimizing risk of predation (Lima *et al.*, 1985).

Norway rats and other rodents appear to retrieve objects for various purposes, since there are several properties of objects that induce retrieval when the animal is in the appropriate motivational state, and these properties are associated with different motivational systems (Wallace, 1979, 1985). For example, hungry Norway rats will retrieve large numbers of food objects (Morgan *et al.*, 1943), while rats of this species that are well-nourished and not inclined to retrieve food will retrieve objects that they can take apart by gnawing or tearing, which may be related to nest building or to discovering novel foodstuff (Tigner & Wallace, 1972; Wallace, 1994).

In line with this general rule, Bindra (1947) showed that domestic Norway rats when deprived of water would retrieve cotton dental rolls, or pledgets, soaked in water. He noted that it was unlikely that the opportunity to retrieve water occurred often enough during the evolutionary history of these animals for this to be a specific adaptation. They were therefore able to respond appropriately on the basis of their experience in the immediate situation. Bindra found that these pledgets were retrieved on the first trial of testing, perhaps too quickly to have been the product of trial and error learning. However, details of acquisition are unclear, and in addition the effects of novelty were not controlled.

Water retrieval may, therefore, serve as an effective demonstration

that retrieval behavior can occur in an appropriate form in a situation that rats would not normally encounter. This paper presents data pertaining to the question of whether water retrieval does, in fact, emerge full-blown, without a period of trial and error. Experiment 1 confirms Bindra's finding using better controls, and includes observations of behavior during the very first opportunity to retrieve following water deprivation.

In this experiment, rats were presented with dental pledgets that were either dry or soaked in water. Following exposure to these objects under conditions of *ad lib* feeding and drinking, the rats were deprived of water and then exposed to the same objects under this condition. A shift to 'water retrieval' that was sufficiently marked and complete would indicate that these animals can in some sense deduce the correct behavior without a period of trial and error with guidance based on feedback from rewards. (As the General Discussion will show, the concept of deduction referred to here does not imply elaborate information processing that might be called "cognitive".)

It might be thought that a more direct test would be to deprive rats of water and, under these conditions, expose them to either wet pledgets alone or to wet and dry pledgets for the first time. However, the results of this test (particularly, the first response on encounter with the objects) would be confounded by novelty effects. Domestic rats retrieve on the basis of novelty, i.e., they pick up and retrieve any small object they have not encountered before, and this effect is strong enough to compete with retrieval based on other object features even under stringent deprivation (Wallace, 1979). However, since it is of interest to compare the behavior of rats that encounter these objects for the first time when they are thirsty, a second experiment was run to test this condition.

EXPERIMENT 1

METHODS

Subjects and Apparatus

Twelve Norway rats of the Sprague-Dawley strain were obtained from Simonsen Laboratories, Gilroy, CA. They were housed individually after arrival, given food and water *ad lib*, and handled daily. They were about 70 days old at the beginning of the experiment. In an initial 30-min emergence test, only two rats emerged; these rats

can, therefore, be considered "shy". Bindra (1948) showed that timidity measured in this way is highly correlated with amount of retrieval. Four rats were dropped after the first five familiarization trials because they would not emerge from their cages. This left eight subjects, but since this experiment uses a within-subjects design, this was sufficient to obtain statistically reliable results.

The apparatus for each animal consisted of its home cage and a wooden alley placed in front of the open cage during a trial, so the rat could run freely between the two. Cages were 25 x 20 x 20 cm. Cage racks were shielded from light on the top and sides and did not move during the experiment. Alleys were 61 x 20 x 20 cm, open at one end, painted light blue inside (reflectance = 0.9) and covered on top with hardware cloth. Each alley had a bin at the end away from the cage, 20 x 5 x 4.5 cm, divided by a wooden partition into two 10-cm compartments. A piece of plexiglas at the bottom of each half-bin insured that dry pledgets were not dampened by seepage from the other compartment. A separate alley was used for each rat. The average illuminance at the alley surface was 40 lux; the illuminance at the cage floor 2.5 cm from the back was always < 10 lux. During the experiment the temperature was 20-23° C.

Retrieval objects were cotton dental rolls, or pledgets, 1.9 cm in length and 0.6 cm in diameter. The original pledgets, purchased from the Patterson Dental Co., Eugene, OR, were cut in half. Half the pledgets were soaked in tap water; the other half were dry. Wet pledgets weighed about 1.7 g, dry 0.2 g. Water for soaking was kept overnight, so its temperature was similar to water in the rats' water bottles. Forty objects of each type were placed in a bin for each retrieval trial, with wet and dry pledgets in separate compartments. For each rat, placement of wet and dry pledgets in left and right bin compartments during retrieval trials was determined by a different Gellerman order. New pledgets were used for each trial and were removed from the cage immediately after each individual trial.

Procedure

Individual daily trials were given at the end of the light part of a 12:12 LD cycle with darkfall at 10 PM. All trials lasted 10 min. Rats were first given a series of familiarization trials with no objects in the bins, until all rats were entering their alleys within 30 s of the beginning of the trial. Because of the timidity of these rats, the first eight familiarization trials after the initial emergence test were run with lower illumination (< 10 lux in the alleys), followed by four trials with

the original illumination.

Retrieval trials began on the day after the last familiarization trial. On each retrieval trial, the number of objects carried to the cage was recorded. On some trials behavioral observations were recorded on score sheets.

The first six retrieval trials were given under *ad lib* conditions. Water deprivation began 24 h after the sixth trial, and the first trial under this condition was given on the following day. During this period, rats were allowed to drink from their water bottles once a day for 10 min. Eight trials were given under these conditions: on Trials 1-5 and 8 rats were allowed to drink from their water bottles immediately after their retrieval trials; on Trials 6-7 they drank before. *Ad lib* drinking was reinstated immediately after the last deprivation trial, and post-deprivation trials began on the next day. Two sets of seven trials were given during the post-deprivation *ad lib* period, separated by five days of rest.

Average water intake for the five days immediately before deprivation was 28 ml for the dark period and 10 ml for the light; during deprivation it was 10 ml (post-trial); during 22 days following deprivation it was 31 ml (dark) and 12 ml (light).

RESULTS

During the first *ad lib* condition, rats retrieved both types of object but showed a definite preference for dry pledgets (Figure 1). Observations of rats before deprivation indicated that less than half the animals retrieved water-soaked pledgets on the first alley entry for a trial, including Trial 1.

After rats were deprived of water, the change in preference was immediate and complete. During the first 5 days of deprivation only two rats retrieved any dry pledgets (≤ 2 on one or two trials). Observations on Trial 1 of deprivation showed that the preference for water-soaked pledgets was evident on the first entry into the alley: on this entry all eight rats picked up and retrieved a water-soaked object. Half the rats first went to the compartment with dry pledgets and contacted these objects, and one first contacted the wet and then the dry pledgets; each of these rats then moved to the side with the wet objects, and immediately picked up a pledget and retrieved it. One animal of the former group did pick up a dry pledget on the initial contact, but after chewing it briefly, it dropped this pledget and moved to the side of the bin with the wet objects. The remaining rats contacted the wet objects on their first encounter, and picked up and retrieved one immediately.

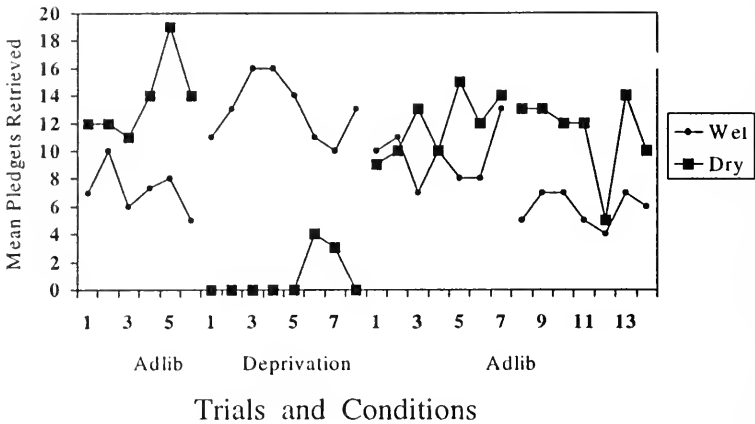


Figure 1. Number of wet and dry pledgets retrieved under *ad lib* drinking and water deprivation (subject-means for each trial). Between Trials 7 and 8 of the second *ad lib* condition there was a five-day break.

On the two days on which water was given before the trial, there was a small but consistent increase in the number of dry pledgets retrieved. In the *ad lib* condition following deprivation, there was an immediate increase in the number of dry pledgets retrieved, but only a slight decrease in retrieval of wet pledgets. During a second post-deprivation series (after a five-day break), retrieval of wet pledgets decreased further, so that the difference was similar to the *ad lib* condition before deprivation. (Bindra [1947] observed a similar slow decline in water pledget retrieval when *ad lib* conditions were reinstated after deprivation.)

Wilcoxon Matched-Pairs Signed-Ranks tests (2-tailed) were carried out to compare objects under each condition. For the first *ad lib* condition, $T(8) = 4$ ($p = .05$); for deprivation with water given after, $T(8) = 0$ ($p = .01$), and before, $T(8) = 4$ ($p = .05$); for successive sets of post-deprivation *ad lib* trials $T(8) = 17$ (ns) and $T(8) = 9$ (ns), respectively. In addition, there were statistically significant ($p \leq .05$) differences between conditions: for both objects, between the first *ad lib* condition and deprivation (water after); for dry pledgets, between water after and water before; for dry pledgets, between deprivation and the following *ad lib* condition.

Observations during the trials showed that under deprivation, retrieval of a wet pledget was always followed by oral consummatory behavior (licking, with some chewing and tearing), although in some

instances the time spent in this activity was very short. During *ad lib*, neither the wet nor the dry pledgets were necessarily the object of oral consummatory behavior after retrieval. On all trials, a number of pledgets were torn apart to some degree, including both wet and dry pledgets during *ad lib*.

DISCUSSION

The present experiment confirms Bindra's (1947) findings: when deprived of water, Norway rats retrieve objects containing water in preference to other objects. The present work shows, further, that under deprivation water retrieval is immediate and consistent, at least when the rats are familiar with the objects; there is no apparent trial and error even during the very first instance of retrieval. It should be emphasized that these results were found for all rats without exception. This suggests that selective retrieval of an object containing water under conditions of thirst is well within the capacity of most rats of this species.

Preference for the dry pledgets in the first *ad lib* condition is probably related to the greater "partibility" of these objects (*cf.* Wallace, 1994), since dry pledgets were pulled apart to a greater extent than wet ones. It is unlikely that it was due to the greater weight of the wet pledgets, since rats can carry much heavier objects (like food pellets) with ease.

This experiment is a demonstration of "latent learning" of the type in which an irrelevant incentive is presented together with a relevant one during the initial training (e.g. see Rashotte, 1979). Viewed in this context, it is a remarkably robust example of such learning, in comparison with results of classical experiments of this type. The latter include cases where no positive result was found or where the results, while statistically significant, were typically small. The difference may be due in part to the fact that, in the present experiment, rats were not initially in a state of deprivation, since there is evidence that this impairs learning of irrelevant incentives (Meehl & MacCorquodale 1948; Rollin 1958). But even in this case, earlier results were not as marked or reliable. A possible explanation of this difference is that the present paradigm fits the response organization of these animals better than the original latent learning situations did, since it is based on a relation between an object property and a species-typical behavior associated with transportable objects.

EXPERIMENT 2

This experiment was designed to observe patterns of responding when rats encounter the wet and dry objects for the first time under water deprivation.

METHODS

Subjects and Apparatus

Ten male Norway rats of the Sprague-Dawley strain were obtained from Charles River Laboratories, Wilmington, MA. They were kept in pairs in plastic tubs after arrival (at 51 days) and transferred to individual cages one week before testing. They were 83 days old on the first retrieval trial of the experiment. Since only two rats emerged within 30 min on an initial emergence test, these rats can be considered "shy". Two rats were dropped during familiarization trials because they would not emerge from their cages.

The apparatus was similar to that of Experiment 1. Cages were stainless steel, 20 x 24 x 19 cm, with solid backs and sides. Alleys were plywood, 18 x 61 x 18 cm, painted light gray (reflectance = .45). At the end of each alley was a bin 18 x 2 cm, divided in half to form compartments each 8.5 cm wide. Average illuminance under regular lighting at the alley surface was 155 lux, at the cage entrance 117 lux, cage back 8 lux. Under dim lighting it was ≤ 5 lux in the alleys. During the time that the rats were tested the temperature was 21-24° C.

Retrieval objects were cotton dental pledgets, 3.8 cm in length, 0.8 cm in diameter (Roeko dental rolls, Size 1). Dry pledgets weighed 0.4 g, wet pledgets 1.9 g. Twenty-five objects of each type were placed in each bin on each trial. Objects were placed in left and right compartments according to four orders (two rats per order) for the four retrieval trials; in terms of placement of wet pledgets these were, RLRL, LRLR, RLLR, and LRRL. As in Experiment 1, new pledgets were used for each rat on each trial.

Procedure

Individual trials were given daily at the end of the light part of a 12:12 LD cycle with darkness commencing at 8 pm. After the initial emergence trial under regular lighting, rats were given four familiarization trials under dim (red) light, then three such trials under

regular lighting. These were 10 min unless the latency to emerge was over one min; in the latter case 10 min were given following emergence. Rats were deprived of water after the first familiarization trial under regular lighting; thereafter, each rat was given 10 min to drink following its daily trial. Four retrieval trials were given beginning on the day after the last familiarization trial. Retrieval trials were 10 min except for one rat on Trial 1 that emerged after 12 min and was given a 20-min trial on that day. On the last familiarization trial and all retrieval trials, behavioral observations were recorded on score sheets.

Average water intake per day for five days immediately before deprivation was 33 ml; during deprivation it was 12 ml (post-trial). It was 60 ml on the day following deprivation and averaged 42 ml on the subsequent eight days.

RESULTS

For all rats, a preference for the wet pledgets developed quickly during the first retrieval trial. Means (per rat) for objects retrieved on successive trials were 11.5, 17.8, 15.8 and 14.4 for wet pledgets, and 2.4, 0.9, 0.3 and 0.3 for dry. Differences in number of objects retrieved on a trial were evaluated with Wilcoxon tests, giving $T(8) = 0$ ($p = 0.01$) for each trial.

On the first retrieval trial, six of the eight rats retrieved a wet pledget initially; in five cases this was on the first entry into the alley. In only two cases was subsequent retrieval restricted to the wet objects. In two cases, rats retrieved several dry pledgets in succession after retrieving (and 'consuming', i.e. licking and chewing) one or two wet pledgets; these rats then switched to wet pledgets for the rest of the trial. Only one rat retrieved wet pledgets exclusively on this trial (although this rat did retrieve a dry pledget on Trials 3 and 4).

On Trial 2, four rats retrieved wet pledgets exclusively, and this number increased to six on Trials 3 and 4. In all but one case, retrieval of dry pledgets on later trials was restricted to single instances in a trial; the exception was a sequence of four retrievals at the beginning of Trial 2.

A partial assessment of the development of this preference was obtained by considering the proportion of rats that picked up an object given that they had contacted it with the snout. This measure has been termed "object seizure: contact" and has been shown to characterize a critical decision in the behavioral sequence underlying object retrieval (*cf.* Wallace, 1997). However, object seizure is not always followed by

retrieval, since decision making is distributed in the behavior sequence (*ibid*). In the present analysis, object seizures were tallied for successive contacts during Trial 1, giving the proportion of those rats that picked up an object on the i^{th} contact. These results, along with the number of rats making an i^{th} contact during this trial, indicate that the tendency to respond on contact in this way was roughly equal for both objects at the beginning of the trial. Subsequently, this tendency increased for the wet objects, while it remained at the same level for the dry objects across several contacts and eventually declined to zero (Table 1). On subsequent trials this tendency was nil in most cases for dry objects even on the first contact. In contrast, in the first deprivation trial of Experiment 1, the proportion of seizure responses for dry pledgets was 0.13 for the first contact and zero thereafter.

Table 1. Proportion of Rats Seizing Object on Successive Contacts on Trial 1 of Experiment 2. Wet, Wet Pledgets; Dry, Dry Pledgets; n, number of rats; S:C, Seizure to Contact Ratio.

	Contact Number										
	1	2	3	4	5	6	7	8	9	10	11
Wet											
n	8	8	8	8	8	8	8	8	8	8	8
S:C	0.8	0.8	0.8	1	1	1	0.9	1	1	1	1
Dry											
n	8	8	8	7	6	3	3	3	2	1	1
S:C	0.6	0.6	0.6	0.9	0.5	0.7	0.7	0	0	0	0

DISCUSSION

Although rats quickly developed a nearly exclusive preference for wet over dry objects in this experiment, the preference was not immediate, as it was in Experiment 1 under similar conditions. Clearly, the rats had to learn to do something in this experiment that they could do at the beginning of the first deprivation trial in Experiment 1. This shows that experience with the objects under *ad lib* conditions in the first experiment was critical for the capacity to respond appropriately under conditions of water deprivation at the first opportunity, i.e. to

substitute 'deduction' for trial and error learning in establishing an exclusive preference for the wet objects.

As in earlier work (Wallace, 1997), learning in this experiment had two aspects. The rats learned to approach the side with the wet objects (reflected in the decline in number of rats making an i^{th} contact with dry objects). They also learned to inhibit retrieval responses occurring after approach to the objects (here, the object seizure response). However, these tendencies by themselves cannot explain the immediate shift in responding under deprivation in Experiment 1, because during the first *ad lib* condition of that experiment the rats tended to approach the dry objects and inhibit responses to the wet ones.

GENERAL DISCUSSION

Bindra (1947) has argued that it is unlikely that water retrieval is a specific adaptation to thirst, since opportunities to retrieve water probably do not occur often enough in the natural state to allow this behavior to be selected. In support of this, it may be noted that, while there are now a number of field studies of this species, none of them include observations of such behavior. At the same time, rats of this species seem to prefer riparian habitats, and they drink readily from water sources (Lore & Flannelly, 1978; Pisano & Storer, 1948; Telle, 1966). Of course, rats will usually obtain water as well as other nutrients from the foodstuff they retrieve, but water itself is probably not important for food retrieval, as shown by the proclivity of hungry Norway rats to hoard dry food pellets. It is significant that in both Bindra's original study and the present work, water was contained in an object that is itself inedible (and which rats showed no signs of ingesting, even while extracting water from it). This sets the problem in high relief, because in this case object retrieval is based on water without reference to any other nutrient. (And there is no question of the rats retrieving cotton rolls because of stimulus generalization or confusion with some nutrient, since under these conditions there was absolutely no retrieval of the same pledgets if they were dry.)

It might be argued that after detecting the wetness of a pledget, a rat would naturally pick it up in order to lick it, and this act of grasping an object while outside a home or refuge provides the stimulus for object carrying. But, in the first place, it is not clear that water detection would be 'naturally' linked to anything but licking. Yet on the first encounter with the objects on Trial 1 of deprivation in Experiment 1, no rat licked the wet pledgets before picking one up, and half the rats

simply picked one up and carried it to the cage without any licking in the alley. (The remaining rats licked the pledget briefly after seizure before carrying it to the cage.) Secondly, object seizure does not automatically lead to carrying. Rats can make the decision of whether or not to carry an object after they have picked it up as reflected in the probability of this response (Phelps & Roberts, 1989; Whishaw, 1990; Wallace, 1997). Thus, in Experiment 1, one rat did pick up a dry pledget initially on Trial 1 of deprivation, but this object was then dropped, and the rat moved to the side with the water pledgets, picked one up and carried it.

The results of Experiment 2 are relevant in this connection because they show that, even if one assumed that water retrieval is a specific adaptation, one could not explain the sudden shift in preference in Experiment 1 on this basis. In this case, rats in the second experiment would have shown an immediate retrieval preference in favor of the wet pledgets without a period of trial and error learning.

These arguments suggest that retrieval of wet objects in Experiment 1 under conditions of thirst was the result of an immediate computation, or 'deduction', based on information about the current situation. Some of this information, i.e., the characteristics and general location of objects in the alley, would have been acquired in previous trials. Other critical information, such as the state of water balance, was presumably based on direct detection.

It must be emphasized at once that the term "deduction" in this context carries no implication of any particular 'cognitive' processes on the part of the rat. In fact, an hypothesis to be presented shortly about the nature of this deduction has a distinct S-R (stimulus- response) flavor. One way to orient one's thinking here is to note that an S-R relation is a kind of deduction. For example, a simple stimulus-response relation like:

$$S_{\text{water}} \Rightarrow R_{\text{retrieval}}$$

(where "retrieval" is shorthand for specific responses such as picking up an object and carrying it that make up the retrieval sequence) can be viewed as a deduction with a single implication, having S_{water} as the antecedent and $R_{\text{retrieval}}$ as the consequent. In other words, all that is implied here by the term "deduction" is a conditional response. This is what is meant by the phrase "behavior as deduction"; conditional responding has the features of a deduction, whatever the basis for this association.

Thus, the issue of whether a rat can represent pertinent conditions in a way that is in some sense "declarative" (Dickinson, 1988) is

irrelevant to the present argument. As I will show, the deductive capacities in evidence here can be handled within a "procedural" (here, an S-R) framework. On the other hand, the information required for this deduction, that was gained during the initial *ad lib* condition of Experiment 1 without apparent overt manifestation, appears to have the characteristics of declarative knowledge. It is worth noting in this connection that in computer science and artificial intelligence, the meaning and status of the distinction between declarative and procedural information is still controversial: some authors argue that it is basic (Genesereth & Nilsson, 1987), while others note that it tends to evanesce when the computational processes are examined closely (Wegner, 1968; Winston, 1977).

If an S-R framework is sufficient, then why speak about deductions at all? The reason is that, according to the present argument, the rat behaves in a manner consistent with a novel deduction that is appropriate to the situation. In doing this it avoids search, or trial and error, in coming up with a solution to its problem. This may be an interesting example of the principle that inference is generally more efficient than search; more familiar behavioral examples are 'built-in' stimulus-response patterns, i.e., species-typical behavior patterns that do not require learning. (Of course, the latter are not novel in the sense used here.) Under the present assumptions, other kinds of object retrieval, e.g., of sweet-tasting or novel objects, could be carried out through the same form of deduction. An earlier experiment is suggestive in this regard. Gross and Cohn (1954) found that rats fed a vitamin-B deficient diet retrieved normal food pellets in greater numbers than ones made from the deficient diet, when the two were presented together. Although details of behavior at the beginning of the experimental tests were not given, a few rats showed an exclusive preference for normal pellets during this period, so they must have selected them from the very beginning of the condition.

All this suggests that the characterization of object retrieval as a simple (stimulus-) response sequence is inadequate. It may be more accurate to describe it as a limited domain of inference expressed in terms of a particular behavior pattern.

An explanation for this deductive ability can be given that is fairly straightforward in principle. We are assuming that the rat's behavior does not embody the following proposition at the outset,

$$\forall_x [(wet(x) \& transportable(x) \& THIRST)] \Rightarrow retrieve(x) \quad (1)$$

where x is some perceived entity, "wet" and "transportable" are features of x , and THIRST is a state of the animal, here represented as an atomic proposition. (Again, this proposition is meant to represent relations embodied in the rat's behavior in some situation; it is not meant to imply that the rat can 'think' about the situation in this way.) However, there is much evidence to indicate that wetness and other properties such as sweetness and novelty all have characteristics referred to as incentive or value under the proper conditions (thirst, in the case of wetness) (Toates, 1986). This can also be represented by an implication:

$$\forall_x [(wet(x) \& THIRST) \Rightarrow incentive(x)] \quad (2)$$

If we then assume that the following implication is already embodied in the machinery of object retrieval,

$$\forall_x [(incentive(x) \& transportable(x)) \Rightarrow retrieve(x)] \quad (3)$$

then $retrieve(x)$, i.e., the overt act of retrieving object x , can be derived from the antecedent of proposition (1) by appropriate substitutions.

The point of the above argument is that, by recoding properties like wetness or novelty into a more general property like incentive and by tying retrieval to this more general 'term', we get 'deductions' in the form of behavior that do not have to be selected for as such. From another perspective, the rat has arrived at a general rule of thumb for retrieving objects in terms of incentive or value instead of more specific rules of thumb in terms of specific object properties, and from this rule it can deduce procedures consistent with policies that it has not had to implement during its previous ontogenetic or phylogenetic history. One must, of course, assume that the incentive-retrieval linkage was originally selected for in some specific context. Given more than one type of object that could be profitably retrieved (e.g., food items and nesting material), an incentive encoding may have led to simpler and more efficient elicitation of object retrieval, as well as providing a common basis for choosing between objects (Wallace, 1997). This latter function may have been a critical selective factor, since a common incentive could support consistent object preferences based on quantitative variations in this factor, while it is not clear that this could be accomplished easily (or at all) given a set of specific adaptations (eg, sweetness-retrieval, water-retrieval). Moreover, a common incentive

factor can (potentially) allow the organism to override the input from an incentive that is immediately present if there is something else in the environment that is preferable, a capacity shown by Norway rats (Wallace, 1997).

It should also be kept in mind that incentive processes serve other functions than supporting object retrieval (*cf.* Toates, 1986), so these processes may have existed before their association with this behavior. Hence, there is nothing in the consideration of possible evolutionary pathways that makes the emergence of a capacity for novel behavioral deductions impossible or even unlikely. To my mind, the alternative, that water retrieval was selected for directly, seems far less tenable.

The deductive properties of object retrieval by Norway rats make this behavior a kind of generalist strategy. However, the present account differs from commonly noted instances of such strategies in the following way. Consider the specialist/generalist dichotomy in the domain of feeding, e.g., a herbivore versus an omnivore. The main difference in this case is between a system specialized to digest certain types of vegetable matter efficiently and a less efficient system that can handle a greater variety of foodstuffs. This difference involves an important tradeoff with respect to adaptability: the generalist does not have the ability to forage efficiently for certain foodstuffs, and here it is outcompeted by the specialist, but if these foods are not available, the specialist perishes. In contrast, in the present case the generalist gives up very little - some extra neural apparatus to recode object features and slightly longer times for decision making, both of which appear to be inconsequential. This gives good reason for expecting that, if the capacity to make behavioral deductions in more general terms evolves, it will displace more specialized strategies. The latter are not adapted to as many conditions and will not outperform the generalist strategy sufficiently in any condition so as to support existence in a separate niche. Therefore, incentive functioning in this generalized fashion may be a fairly common feature of animal behavior.

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CONTEXTUAL DISCRIMINATION AFTER NONREINFORCED PREEXPOSURE TO THE CONTEXT

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ABSTRACT: Rats were trained on a contextual discrimination after nonreinforced preexposure to both contexts. In Experiment 1, where contexts differed in terms of tactile and visual stimuli, preexposure retarded subsequent discrimination by comparison with non preexposed controls (latent inhibition). In Experiment 2, where contexts differed only in terms of visual cue, discrimination was facilitated in preexposed animals (perceptual learning). Food was used as reinforcer and anticipatory activity as dependent measure. These results suggest that contextual similarity influences the outcome of nonreinforced preexposure.

RÉSUMÉ: Se entrenaron ratas en una discriminación contextual apetitiva después de preexposiciones no reforzadas a ambos contextos. En el Experimento 1, en el cual los contextos diferían en características visuales y táctiles, la preexposición produjo un retraso en la discriminación, comparada con un grupo no preexpuesto (inhibición latente). En el Experimento 2, en que los contextos eran diferentes en claves visuales, la preexposición facilitó la discriminación (aprendizaje latente). Se utilizó alimento sólido como reforzador y la ambulación anticipatoria como medida dependiente. Estos experimentos sugieren que la similitud de los contextos preexpuestos producen mayor facilidad o retraso en su discriminación posterior.

INTRODUCTION

Nonreinforced preexposure to a stimulus can affect its subsequent conditioning either retarding acquisition (i.e. latent inhibition; Lubow & Moore, 1959, Lubow, 1989), or facilitating acquisition (i.e. perceptual learning; Gibson & Walk, 1956; Fanselow, 1990; Kiernan &

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Westbrook, 1993). Chamizo and Mackintosh (1989) and Trobalon, Sansa, Chamizo and Mackintosh (1991) have demonstrated that one training variable determining whether preexposure leads to retardation or facilitation of discriminative learning is the proportion of features or elements S+ and S- share in common. In one of their experiments, rats were preexposed to a T-maze in which the arms were differentiated by the type of floor (either rough or smooth) and were subsequently trained in a tactile discrimination task based on those stimuli. The preexposed rats learned the discrimination faster than non preexposed controls. By contrast, when the arms of the maze differed in terms of the floor and also in terms of brightness of the walls (white or black), preexposure led to retardation, relative to nonpreexposed controls.

These results favoured an interpretation based on a model developed by McLaren, Kaye, and Mackintosh (1989), specifically designed to explain perceptual learning. According to this model, the greater the similarity between two stimuli, the more likely it is that their common elements will be sampled in each trial. Because nonreinforced sampling decreases the associability of the sampled elements, relatively similar stimuli will become more discriminable thus yielding perceptual learning. When the stimuli are more different from each other, then their common elements will be less likely to be sampled and thus subsequent conditioning will be retarded yielding latent inhibition. There is a second mechanism that could be responsible for this differential outcome. According to McLaren *et al.* (1989) the early trials of preexposure will produce some tendency to generalization between two stimuli caused by the formation of excitatory associations between their common and unique elements. Further trials will cancel this generalization establishing inhibitory connections between the unique elements of the stimuli. The greater the similarity between two stimuli, the greater the inhibitory learning that will be formed between them. Thus, preexposure will produce facilitation of discriminative learning if stimuli are very similar, but not if stimuli are more different from each other. Both of the mentioned processes are based on the degree of similarity of the stimuli.

The present experiments were designed to test the same hypothesis as it applies to classical contextual conditioning rather than to spatial instrumental conditioning. Unlike discrete stimuli, which have a clear onset and offset and precede the presentation of the reinforcer closely, contextual stimuli are constantly present characterizing the location where conditioning takes place, rather than the point in time when the reinforcer will be presented. According to most contemporary theories of conditioning, contextual and discrete stimuli follow the same

learning principles (i.e., Rescorla & Wagner, 1972; Pearce, 1987; McLaren *et al.*, 1989). Moreover, McLaren *et al.* (1989) model does not explicitly differentiate between discrete and contextual stimuli. It was therefore expected that the acquisition of a contextual discrimination would be retarded by preexposure, when the contexts were markedly different from each other, but facilitated when the contexts were relatively more similar to each other. In the two experiments, similarity was manipulated by increasing the number of elements that are common to the signals for reward and non-reward.

EXPERIMENT 1

The two contexts used in the present experiment differed in terms of visual and tactile cues, thus presumably having relatively few elements in common. Therefore, it was expected that, after nonreinforced preexposure, the rats would find their discrimination to be relatively more difficult than control rats not preexposed to the contexts. Previous experiments have shown that contextual conditioning based on the presentation of food can be measured in terms of general activity. Mustaca, Gabelli, Papini & Balsam, (1991, Experiment 1) measured a wide range of behaviours after a differential contextual training using rats as subjects and found that activity was the only behaviour that yielded a consistent pattern across sessions and contexts. Subjects exhibit significantly more activity (walking, running, circling, or jumping) in the presence of a context paired with food than they did in the presence of a different context in which food was never presented. The increase in general activity in anticipation of food presentation is similar to the behavioural changes that have been observed in pigeons (Durlach, 1982, 1983) and ringdoves (Balsam, 1982 1985) under similar circumstances. Consequently, these same features were used in the experiments reported here.

METHOD

Subjects

The subjects were 12 adult Wistar rats, all female and experimentally naive. They were approximately 90 days old at the start of the experiment. Ten days before the experiment, the subjects were transferred to individual cages with water freely available. During 10

days, the daily amount of food was gradually reduced until their weights were lowered to an 80-85% of the individual ad libitum weights. The colony was under a 12:12 cycle of light and darkness, with light from 7:00 to 19:00 hr.

Apparatus

Subjects received training in 2 similar conditioning boxes measuring 52 x 31 x 35 cm (length, width, height). The wall facing the observer, as well as one of the lateral walls and the ceiling, were made of translucent Plexiglas. The other walls and the floor were painted black. One of the black walls contained a tube through which the reinforcer (0.15 g pieces of commercial cookies) was manually administered. The tube protruded 1.5 cm within the box, and was located at 5 cm above the floor and in the middle of the wall. The reinforcer fell directly on the floor. A speaker located in the upper right corner of the same wall provided masking white noise. A light (60 W) located 40cm above the floor of the laboratory provided diffuse illumination.

The preceding description applies to context A. Several elements were added to produce context B. A piece of cardboard was placed in the wall containing the reinforcer tube. This cardboard had vertical red and white stripes, 1.5 cm wide. A rough grid was placed on the floor. A diet Pepsi can, filled with sand, was located 10 cm. away from the reinforcer tube and directly in front of it. Finally, an orange bulb (12 W) was placed in the upper left corner of the same wall containing the reinforcer tube. (This bulb was turned off for context A.)

Previous experiments run in our laboratory show that pieces of commercial cookies (Lincoln, Nabisco-Terrabusi. Main ingredients: vanilla and lemon flavour, flow, sugar, fat, starch, glucose extract, and salt) can be used as appetitive reinforcers and that contexts A and B are easily discriminated by rats (see Pellegrini, 1997; Mustaca & Pellegrini, 1996).

Procedure

Subjects were randomly assigned to 2 groups (n=6) according to whether or not they received preexposure. Group PE received 10 sessions in each of the two contexts, at a rate of 2 sessions per day, separated by an interval of 20 min. These sessions lasted 5 min, and no food was presented. The subjects in group C were similarly handled but were not exposed to the contexts.

During acquisition, all subjects received 10 sessions of training in each of the contexts. Context A was always reinforced whereas context B was always nonreinforced. In each of the reinforced sessions, food was delivered according to a variable time 30 s schedule. Although the first session was reinforced for all subjects, the rest of the sessions in contexts A and B were alternated at random with the only restriction that one exposure to each context was administered per day.

Behavioural observations were carried out in sessions 1-2, 9-10 and 19-20 (one session in each context for any given pair) of the preexposure phase, and in each session of the acquisition phase. These observations lasted for 2 min and thus session length was 7 min during the 6 sessions of preexposure listed above, and during all the acquisition sessions. An observer recorded every 5 s whether or not (1/0 sampling) the rat was active. "Activity" was defined as any movement of the limbs (e.g., walking, running, circling, or isolated movements of any number of limbs). This observation technique is frequently used in our laboratory. Reliability has been estimated against naive observers (agreement above 95%; Mustaca & Pellegrini, 1996) and against an automatic device (Pearson's coefficient of correlation $r=0.81$, $p<.0001$; Pellegrini, 1997). In view of the relatively high level of agreement, reliability was not explicitly estimated in the present experiments. No food was delivered during the 2 min of behavioural observations.

RESULTS

The level of activity observed in each of the two contexts in Group PE, during preexposure sessions, decreased as preexposure progressed, but there were no appreciable differences between contexts. A Context \times Session analysis of variance yielded only a significant effect of Session [$F(2,10)=25.27$; $p<.001$]. The effects were not significant for Context ($F<1$) or for the Context \times Session interaction [$F(2,10)=1.75$].

All animals ate the food delivered during training sessions. Figure 1 shows the main results of the acquisition phase for each group and session. The dependent variable was a discrimination index (DI) obtained by subtracting the activity score in context B (nonreinforced) from that obtained in context A (reinforced). As the DI becomes more positive, the frequency of activity in the reinforced context increases relative to the activity observed in the nonreinforced context. As Figure 1 shows, discrimination was retarded in Group PE, relative to Group C. A Group \times Session analysis provided support for this conclusion in the form of a significant Group effect [$F(1,10)=17.34$; $p<.002$]. There was also a significant Session effect [$F(9,90)=10.20$; $p<.0001$]. The Group \times Session interaction was not statistically reliable [$F(9,90)=1.78$; $p<.08$].

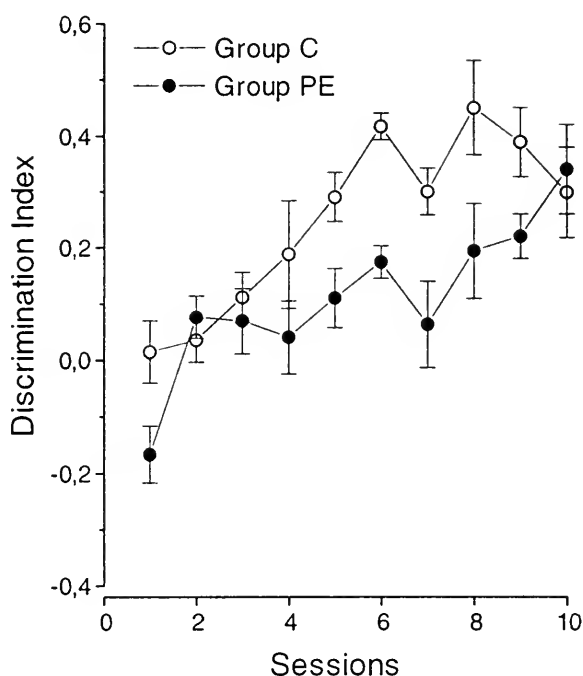


Figure 1. Contextual discrimination in groups preexposed (PE) or not (C) to the context during a prior phase. Training contexts differed in terms of visual and tactile cues. See text for a definition of the discrimination index.

EXPERIMENT 2

The contexts to be discriminated in the present experiment were made more similar by removing elements from context A in the previous experiment. As already noted, McLaren *et al.* (1989) hypothesis assumes that greater contextual similarity implies a larger proportion of common elements. Preexposure should then serve to reduce the associability of these common elements to a greater extent than that of the unique elements. In turn, this should lead to perceptual learning, that is, the discrimination of the stimuli should be subsequently facilitated.

METHOD

Subjects and Apparatus

The subjects were 14 rats of the same characteristics as in Experiment 1. Maintenance conditions and deprivation were as already described.

The conditioning boxes were those already described. Context B was created by placing the board with the red and white stripes against the wall with the food-delivery tube. Context A was the same as in the previous experiment.

Procedure

Rats were randomly assigned to two groups ($n=7$). There were two procedural differences with respect to Experiment 1. First, the assignment of subjects to context A and B was counterbalanced. In each group, 4 rats were trained in an A+/B- discrimination, and 3 rats were trained in a B+/A- discrimination. Second, there were a total of 28 discrimination sessions, 14 sessions with each of the two contexts, instead of 20 sessions as in Experiment 1. More training sessions were run because this discrimination was more difficult than the previous one, given the similarity between the two contexts.

RESULTS

For Group PE, the frequency of activity in preexposure sessions 1-2 was higher in the context that was later to become the reinforced one, than in the negative context. However, activity level decreased in preexposure sessions 9-10 and 19-20, in both contexts, and it became nondifferential. A Context \times Session analysis indicated a significant interaction [$F(2,12)=5.41$; $p<.001$], product of the initial differences across contexts, and also a significant habituation effect across sessions [$F(2,12)=15.31$; $p<.001$]. The simple effect of Context was not significant [$F(1,6)=2.76$].

By the third session all animals ate the reinforcers immediately after delivery. Figure 2 shows the performance of both groups during the 14 sessions in each context in terms of the DI. As anticipated, discriminative performance progressed faster in Group PE than in Group C, indicating that the nonreinforced preexposure facilitated the subsequent discrimination of these contexts. A Group \times Session

analysis of these indices supports this conclusion. There were significant Group [$F(1,12)=5.63$; $p<.03$] and Session effects [$F(13,156)=2.45$; $p<.05$], and also a significant Group x Session interaction indicating the faster acquisition by Group PE than Group C [$F(13,156)=2.46$; $p<.005$].

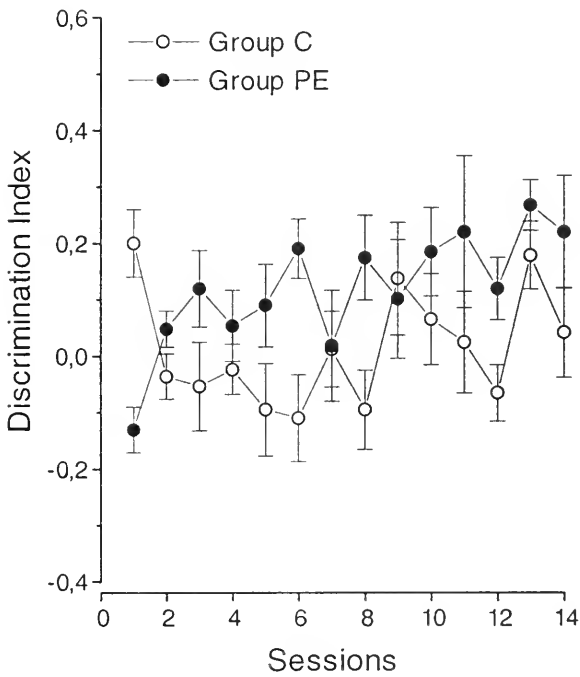


Figure 2. Contextual discrimination in groups preexposed (PE) or not (C) to the context during a prior phase. Training contexts differed in terms of visual cues. See text for a definition of the discrimination index.

DISCUSSION

The main results of the present experiments were that, relative to the non-preexposure treatment, nonreinforced preexposure to the

context had opposite effects depending on the degree of similarity of the contexts. When the contexts were made relatively more dissimilar by the addition of stimuli, the subsequent discrimination was retarded. This effect is akin to latent inhibition (Lubow & Moore, 1959). By contrast, when the contexts were more similar, preexposure facilitated their discrimination, thus yielding a perceptual learning effect.

Because in the present experiments conditioning was assessed in terms of anticipatory activity, and because the level of activity during preexposure habituated in both experiments, it could be argued that these effects could be the simple consequence of differential habituation in Group PE and C. Habituation of ambulation is known to occur in many different situations. This explanation would lead one to predict lower activity levels generally in the groups preexposed to the contexts and could, perhaps, offer an alternative account for the results of Experiment 1. In that experiment, discriminative performance was delayed by the preexposure treatment (see Figure 1). However, this explanation cannot account for the facilitatory effect of preexposure observed in Experiment 2, when the contexts were more similar. In other words, habituation should occur perhaps even faster and to a larger extent, when the contexts are similar because there is the possibility of stimulus generalization (Thompson & Spence, 1966).

Nonetheless, greater contextual similarity actually led to faster acquisition after preexposure than after the control treatment.

Another potential alternative, at least for Experiment 1, is related to the lack of counterbalance of contexts during the acquisition phase. Context A was always reinforced whereas context B was nonreinforced. Perhaps a perceptual bias contributed to the discrimination above and beyond the contribution of preexposure. However, this possibility seems unlikely; previous experiments with these contexts have shown their equivalence (Mustaca & Pellegrini, 1996).

In several studies employing taste aversion (Hall & Channell, 1986), spatial learning (Chamizo & Mackintosh, 1989; Trobalon *et al.*, 1991; Rodrigo *et al.*, 1994) and an appetitive licking procedure (McLaren *et al.*, 1994), it has been strongly suggested that the associations formed within contextual cues during preexposure training are critical for determining whether preexposure will facilitate or retard subsequent conditioning. Furthermore, these investigations are consistent with the idea that one process underlying the effects of preexposure on subsequent discriminative learning is the differential loss of associability by common and unique elements. The results of the present experiments are in agreement with this interpretation and find similar effects using a different training procedure and only contextual

cues as the conditioned stimulus. Therefore, they suggest the generality of this phenomenon.

The emphasis placed by McLaren *et al.* (1989) model on contextual similarity and complexity demands more precise ways of determining these contextual properties. Similarity could be varied more precisely by changing the salience of a single element in independent groups. Such manipulations are needed for a more precise testing of the model's view of contextual conditioning.

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LEFT HAND ADVANTAGE FOR PREY CAPTURE IN THE GALAGO (*GALAGO MOHOLI*)

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ABSTRACT: Efficiency of hand use in nonhuman primates is often difficult to assess because of the relatively small number of responses made with a nonpreferred hand. The present study compared measures of reach efficiency in 8 galagos (*Galago moholi*), 4 left-hand preferent and 4 right-hand preferent subjects, tested in a reach apparatus designed to elicit equal numbers of responses by the left and right hands. The effect of variant or invariant target placement within sessions was also assessed by the use of both blocked and randomized trials. Efficiency was defined in terms of the percentage of successful reaches and the average duration of time required for reach execution. There was no effect of target variance on strength of hand preference or on either measure of performance efficiency. Preferred and nonpreferred hands did not differ with respect to these two measures. There was also no difference in the percentage of successful reaches between the left and right hands. However, for 7 of 8 subjects the left hand generated faster reach times than did the right hand, regardless of hand preference. The greater execution speed with the left arm/hand is interpreted as exemplifying a lateralized neural advantage for the execution of ballistic reaching in galago species. The highly consistent timing of this prey capture behavior in the galago supports the view that this arm/hand movement is ballistic in type.

The search for the evolutionary origins of human laterality has been greatly stimulated by the comparative study of lateralized behaviors in nonhuman primates (Bradshaw & Rogers, 1993; Ward & Hopkins, 1993). Lateral hand preference in simple food reaching has been demonstrated in individuals of many species of prosimian (Ward, 1995) and anthropoid (Kaplan & Rogers, 1994; Hook-Costigan & Rogers, 1996; McGrew & Marchant, 1997; Hopkins, 1996) primates. Hand preference has generally been characterized by the relative frequency of right or left hand use in simple food reaching. However, this measure does not assess possible differences in the performance capacities of the

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two hands. Thus, it is often unclear whether a preference for using one hand in a given task is associated with enhanced performance.

When assessment of the performance capabilities of the two hands is undertaken, analyses typically compare the accuracy and/or speed of performance for each hand, thereby providing an indicator of the relative efficiency of each hand. Frigaszy and Mitchell (1990) examined both preference and performance measures of handedness in capuchin monkeys (*Cebus apella*). The preferred hand for performing both unimanual and bimanual tasks was identified and the movement time of the hand performing the task was calculated. This study revealed that, at least for the unimanual task, movement times were significantly faster for the preferred hand. However, conclusions from the results of this study must be somewhat limited by the small number of responses made with the nonpreferred hand. Likewise, in studies of galago reach preference (Larson *et al.*, 1989; Dodson, *et al.*, 1992), direct comparisons of the efficiency of the two hands was also problematic because of the small number of reaches attempted with the nonpreferred hand during testing. When tested in an unrestricted environment in which galagos could freely position themselves in relation to the food, the nonpreferred hand was used in food retrieval less than 20% of the time. Such unequal response samples for the preferred and nonpreferred hands render performance comparisons between the two hands inappropriate.

The galago is a useful model for examining the relative efficiency of preferred and nonpreferred hands, or of the left and right hands, because it has a specialized type of reach that can be timed to provide a measure of efficiency. In the wild, about 80% of the galago's diet consists of insects that are captured by means of a rapid, stereotyped action often referred to as a "smash and grab" movement (Bishop, 1964). It has been suggested that such ballistic capture movements are controlled by a feed-forward or off-line control process that, once initiated, is not modifiable (MacNeilage *et al.*, 1987). In support of this view is our laboratory experience that galagos have never been observed to alter the trajectory of a reach once initiated. We have also observed that when galagos execute a ballistic reach and miss the prey, they often swing the empty, closed hand back to the mouth and even chew once or twice as though the capture had been successful. If the reach used by the galago to retrieve food from a testing apparatus is indeed ballistic in nature, then the amount of time necessary to complete such a reach should be highly consistent from trial to trial. Because the hand with the faster reach time would have an advantage in capturing prey, this behavioral measure provides an ecologically valid

way to compare the performance parameters of the two hands.

The present study evaluated performance in a population of galagos for whom hand preference had been previously established. A testing apparatus was designed to promote the equal use of both hands. The apparatus contained three food cups, one mounted on each of the two side walls and the third placed in the center of the front panel. Perhaps because of the narrowness of the testing apparatus, the galagos did not position themselves directly facing the side food cups. Rather, they executed across-body reaches, using the hand contralateral to the baited cup. Efficiency was evaluated both in terms of the number of successful reaches made by each hand and the amount of time necessary to complete these reaches. Additionally, we examined the possibility that the strength of hand preference for reaching may be influenced by the predictability of the food location. It has been suggested that delivering such rewards in rapid succession, as in a single bout, may induce postural adjustments that bias responding (Marchant & McGrew, 1991). For example, if the same food cup is repeatedly baited, the predictability of the food location may promote the formation of a path habit and an associated reaching posture, thereby artificially inflating the strength of that animal's hand preference. This experiment therefore included sessions in which the placement of the food was varied from trial to trial.

METHODS

Subjects

Subjects were 8 lesser galagos (*Galago moholi*), 5 males and 3 females, averaging 165 g. Four of the animals were wild caught (estimated age at testing > 7 years); the remaining animals were born in the colony at The University of Memphis (mean age at testing 4.5 years). Four male subjects had been determined to be left-hand (LH) preferent and four subjects (one male, Bobby; 3 females, June, Leadtree, and Morgan) to be right-hand (RH) preferent in previous studies (Larson *et al.*, 1989; Dodson *et al.*, 1992). Subjects were housed individually and were maintained on a 12/12 hr light/dark cycle (lights on at 8 pm). Immediately following each daily testing session, the galagos were fed a diet of Purina High Protein Monkey Chow (Ralston-Purina, St. Louis, MO) with mixed fruits and vegetables. All subjects were allowed ad lib access to water. Subjects were treated in accordance with state and federal guidelines.

Apparatus

All experimental sessions were conducted in a clear Plexiglas testing box, shown in Figure 1. A 5-cm diameter food cup was inset 17 cm above the floor on each side wall of the box, as well as the center wall opposite the entrance. A stainless steel carrying cage (10 x 10 x 25.4 cm) served as a start box, which was placed adjacent to the entrance of the testing box.

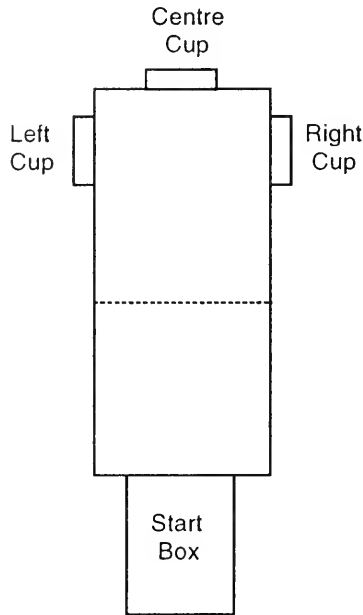


Figure 1. Diagram of the reach apparatus. Three circular clear Plexiglas food cups (2.5 cm in depth) were mounted in the apparatus, one centered in the front wall and one each on the left and right walls positioned 2 cm from the front wall. A 10 cm square opening in the rear wall of the box provided entrance into the testing apparatus. One half of the top panel apparatus was hinged to permit baiting of the food cups.

Procedure

All experimental sessions were videotaped from an overhead view to provide a permanent record for later analysis. A time and date generator indicated elapsed-time (to .01 sec) directly on the videotape. At the start of each trial, the appropriate food cup was baited with a mealworm (*Tenebrio* larvae). The subject was trained to leave the

startbox and approach the food cups to retrieve the mealworm, then to return to the startbox and await the next trial. Thirty completed trials marked the end of each daily session.

Testing Conditions. Each subject completed 8 sessions of 30 trials each for a total of 240 reaches distributed equally across each of the three food cups. Sessions 1-6 comprised the constant locus experimental condition (CON), in which the placement of the mealworm remained constant within each session but varied across sessions. During sessions 1 and 2 the center cup was baited for all animals. Sessions 3 through 6 were counterbalanced so that for 4 subjects (2 LH preferent, 2 RH preferent) the left cup was baited during sessions 3 and 4 and the right cup during sessions 5 and 6. This sequence was then reversed for the remaining 4 subjects. This resulted in a total of 180 trials (60 trials for each food cup) during the CON condition. The final two sessions comprised the variable locus experimental condition (VAR). During each of these sessions, the food cup that was baited was varied from trial to trial according to a pseudorandom schedule so that each cup was baited 10 times, for a total of 30 trials per session. This resulted in a total of 20 trials for each food cup during the VAR condition.

Scoring Categories. The videotapes of each subject's experimental sessions were reviewed to determine the preferred hand for reaching into each of the three cups. For each trial, mealworm retrieval was scored as either right unimanual (R), left unimanual (L), bimanual (B), or mouth (M). Unsuccessful reaches were scored when subjects failed to grasp the mealworm from the cup.

Because the bushbaby's entire body was typically moving forward in conjunction with the forward motion of the arm during the reach, the beginning of the reach could not be defined as the point in which the arm began to move forward. After examining the videotapes of all subjects, a common sequence of movements characteristic of the ballistic reach was identified. As the bushbaby moved toward the foodcup, the hand used to retrieve the mealworm was raised to approximately shoulder height. At this point, the fingers of the hand were closed with the elbow positioned close the body. The elbow then moved abruptly away from the body laterally and the fingers of the hand began to spread apart. The hand then accelerated toward the mealworm with the fingers continually spreading farther apart. Upon contact with the mealworm the fingers closed immediately around it.

The amount of time required to complete each successful reach was determined using a frame-by-frame analysis of the videotaped sessions. The stopwatch on the videotape was used to determine the elapsed time subtended by each successful reach. The beginning of the reach was

defined as the video frame in which the elbow moved laterally away from the body. For each reach, the videotape was advanced to this point and the time on the stopwatch was recorded. The videotape was then advanced to the frame in which the bushbaby's fingers closed around the mealworm. The stopwatch reading from this frame was used to determine the elapsed time between the start and the finish of the reach. All reach time values were determined in hundredths of a second. The videotape was recorded at a speed of 33 frames per second; therefore, the margin of error for determining the start or finish of each reach was calculated to be approximately .03 sec.

To establish how reliably reach times were determined by the observer, 10% of the sessions were randomly chosen and reviewed by a second observer, who independently determined the time required to complete all successful reaches in these sessions. A Pearson correlation revealed a high degree of correspondence between reach times as scored by the two observers ($r = 0.862$, $p = 0.001$).

RESULTS

Three behavioral measures were used to analyze performance in this task: (1) the strength of the preference for using one hand over the other; (2) the time required for each hand to complete successful reaches; and (3) the reach efficiency of each hand, calculated by dividing the number of successful reaches by the total number of reaches (successful and unsuccessful). The preferred hand for retrieving mealworms from each of the three food cups was determined by the total number of right- and left- hand reaches into each cup.

To determine if the strength of preferred-hand use was affected by the predictability of the food location, the overall percentage of preferred-hand use (% P) during the CON and VAR experimental conditions were compared. No significant difference was found between the two conditions ($M_{\text{CON}} = 64.8$, $SD = 5.9$; $M_{\text{VAR}} = 61.3$, $SD = 6.42$), $t(7) = 1.97$, n.s. The efficiency of hand use in the CON and VAR conditions was also examined. Very few misreaches were made; hence, data from all three food cups were combined to compute an overall reach efficiency percentage for each subject's preferred and nonpreferred hand. No difference was found in the reach efficiency percentages between the CON and VAR conditions for the preferred hand ($M_{\text{CON}} = 94.2\%$, $M_{\text{VAR}} = 92.1\%$), $t(7) = 1.30$, n. s. However, the reach efficiency of the nonpreferred hand was slightly lower for the CON condition ($M = 89.3\%$) than for the VAR condition ($M = 93.1\%$), $t(7) = 2.47$, $p < 0.04$.

Finally, reach durations in the CON and VAR conditions were examined. To control for differences in reaching distance, only successful cross-body reaches to the side cups were compared and reaches toward the center cup were not included in this analysis. For each hand, the individual durations for all successful cross-body reaches were combined and the mean reach duration was calculated. These mean reach durations in the CON and VAR conditions were not significantly different from one another for either the preferred hand, $t(7) = 1.95$, n.s., or the nonpreferred hand, $t(7) = 2.30$, n.s. Likewise, no differences between the CON and VAR conditions were found in the mean durations of either right-hand reaches, $t(7) = 2.30$, n.s., or left-hand reaches, $t(7) = 1.92$, n.s.

Because a significant difference between measures for the CON and VAR experimental conditions was found in only one of the five comparisons, data from the two conditions were combined for further analyses. Table 1 provides a list of the percentages of preferred-hand use for each of the three food cups. The design of the testing apparatus resulted in the use of the right hand for the majority of reaches into the left food cup ($M = 96.7\%$ of all right-hand reaches) and the use of the left hand for the majority of reaches into the right food cup ($M = 94.2\%$ of all left-hand reaches). The hand which subjects preferred to use when reaching into the center food cup was found to be the same hand that had been designated as preferred during previous handedness testing (Dodson, *et al.*, 1992; Larson, *et al.*, 1989). The preferred hand therefore remained constant across these testing periods.

Table 1. Strength of Preferred Hand Use for Reaching into the Left, Center and Right Food Cups. PH = preferred hand classification as right- (R) or left- (L) preferent. %R = percentage of right hand use; %L = percentage of left hand use; %P = percentage of preferred hand use.

Name	PH	Left Cup	Center Cup	Right Cup
		%R	%P	%L
Buckwheat	L	93.8	97.5	100
Chewbacca	L	87	83.8	100
Vincent	L	96.3	100	100
Winky	L	100	96.3	100
Bobby	R	98.8	61.3	93.8
June	R	100	93.8	86.3
Leadtree	R	97.5	62.5	83.8
Morgan	R	100	69.7	89.5
Group Mean		96.7	83.1	94.2

The relative efficiencies of the preferred and nonpreferred hands were assessed by comparing the percentages of the total successful reaches with each hand. The overall reach efficiency percentage (RE%) was calculated from reaches into all three cups for both the preferred and nonpreferred hands (see Table 2). Although the RE% for the preferred hand ($M = 92.8\%$) was higher than that of the nonpreferred hand ($M = 89.7\%$), the difference was not statistically significant, $t(7) = 1.41$, n.s. We also calculated the RE% for the left and right hands. As with the preferred/nonpreferred hand analysis, the difference between left and right hands was not significant, $t(7) = 0.08$, n.s.

The movement times of successful cross-body reaches were also compared between hands. For each hand, the individual durations of all successful reaches were combined and averaged. A within-subjects t -comparison of each subject's mean reach times for the preferred and nonpreferred hands revealed no difference between them, $t(7) = 1.00$, n.s. However, the average time required by the left hand ($M = 0.1586$ sec) to complete a successful reach was significantly less than that required by the right hand ($M = 0.1694$ sec), $t(7) = 2.74$, $p < 0.029$. As can be seen in Table 3, the left hand advantage in reach time was exhibited by 7 of the 8 galagos.

Table 2. Comparison of Successful Reaches (#S), Misreaches (#M) and Reach Efficiency Percentage (RE%), for the Preferred and Nonpreferred Hands. PH = preferred hand classification as right- (R) or left- (L) preferent.

Name	PH	Preferred Hand			Nonpreferred Hand		
		#S	#M	RE%	#S	#M	RE%
Buckwheat	L	163	21	88.6	77	13	85.6
Chewbacca	L	156	6	96.3	73	0	100
Vincent	L	163	3	98.2	77	12	86.5
Winky	L	157	12	92.9	83	7	92.2
Bobby	R	133	16	89.3	107	29	78.7
June	R	167	1	99.4	73	7	91.3
Leadtree	R	141	14	90.9	99	5	95.2
Morgan	R	134	20	87.0	88	12	88.0
Group Means				92.8	89.7		

Table 3. Comparison of the Mean Duration (Sec) of the Ballistic Reaches with the Left and Right Hands. N = number of reaches used in computing the mean speed.

Name	Left Hand			Right Hand		
	Mean	SD	N	Mean	SD	N
Buckwheat	.1114	.0270	80	.1219	.0270	75
Chewbacca	.1903	.0742	80	.1963	.0605	60
Vincent	.1791	.0390	80	.2034	.0513	77
Winky	.1290	.0280	80	.1536	.0451	80
Bobby	.1141	.0269	75	.1199	.0279	79
June	.1645	.0208	69	.1684	.0228	80
Leadtrees	.1760	.0266	67	.1959	.0377	78
Morgan	.2038	.0245	68	.1961	.0255	80
Group Mean	.1586	.0357		.1694	.0343	

DISCUSSION

The apparatus employed in this study was highly successful in providing equivalent samples of left and right hand use and thereby permitted comparison of the efficiency of hand use in terms of lateral preference. The results suggest that hand preference, per se, is not a factor in the efficiency of this type of ballistic prey capture; neither reach duration nor prey capture was enhanced as a function of lateral preference. The left hand, however, did require significantly less time to complete a reach than did the right hand across our sample of subjects. The durations of left-hand reaches were shorter in seven of the eight animals tested, four of which were left-preferent and three of which were right-preferent.

The results of this study show that the movement time of the ballistic reach is relatively invariant in the right and left hands of a given individual. Although this suggests a feed-forward type of motor response that might be expected to be hard-wired in the nervous system, it is possible that experiential factors may influence speed of movement. For example, the one galago, Morgan, who demonstrated a slightly faster right-hand movement time, had, prior to inclusion in the present study, undergone extensive testing in a visuospatial reach task in which she used the right hand almost exclusively. This task required the animal to retrieve a food reward from a moving turntable, the speed of which was gradually increased to determine the asymptotic level of

performance. This intensive right-hand practice may explain Morgan's faster right-hand performance relative to the other subjects. It is possible that in this case an endogenously lateralized characteristic was modified by experience. A study of lateralized foraging patterns in the gentle lemur (*Haplemur griseus*) found that those patterns which were most commonly used were executed more quickly (Butler *et al.*, 1995), a response time advantage which was perhaps the result of rehearsal of specific patterns of feeding.

The left hand superiority in movement time does seem to constitute a lateral advantage for the execution of movements that require quick response. It has been shown in cats that reach durations are shorter for the preferred paw than for the nonpreferred paw (Fabre-Thorpe *et al.*, 1993). Furthermore, cats that are lateralized in this action tend to prefer their left paws and have shorter movement times than cats that do not exhibit lateralized reaching behavior. Such laterality may thus have adaptive value, as quicker reaches for prey may enhance success in predation. Humans have also been shown to produce ballistic responses faster with their left hands (Guiard *et al.*, 1983; Azemar *et al.*, 1990). A left side advantage in ballistic movements may therefore prove to be a conservative evolutionary trait. These results are also supportive of the theory of MacNeilage *et al.* (1987) that proposes an endogenous superiority for visually-guided reaching by the left hand in prosimians.

The ballistic character of the galago reach, first suggested by Bishop (1964), is confirmed in this study by the response time invariance. Although there was some variability in the average movement time between subjects (ranging from a low of 0.1167 sec to a high of 0.1999 sec), the standard deviations for left- and right-hand mean durations for each subject shown in Table 2 confirm that the individual mean durations were remarkably uniform. In fact, the average standard deviation for both left-hand (.0357 sec) and right-hand (.0343 sec) reaches approximated the estimated margin of error (.03 sec) for determining the start or finish of each reach from the videotape still-frame (see Methods section). The findings therefore support the contention that these movements are quite invariant in their timing as would be expected for a feed-forward ballistic system.

Although only one species was examined in this study, I propose that this left-hand functional specialization for feed-forward rapid reaching movements may be characteristic of all galago species. Reach efficiencies were also determined for one left-preferent *Galago senegalensis braccatus*, a larger species of galago. This galago was the only one of its species available to us and was old and in failing health. Reach durations for this animal, Weisel, were substantially greater than

the mean reach durations for the *G. moholi*. However, it is important to note that data from this animal were consistent with the data from *G. moholi* with regard to the direction of lateral advantage. Weisel's mean reach duration was shorter for the left hand ($M = 0.3002$, $SD = 0.1244$) than for the right ($M = 0.3285$, $SD = 0.0843$). Thus, although species differences in absolute reach durations may exist, this result suggests that a left-hand superiority for movement time may be found across galago species.

To this point in the discussion, behavioral advantage in prey capture has been couched solely in terms of the greater speed of the left hand in execution of the ballistic reach. It might be asked: if left specialization has adaptive significance for feeding, why in this study was no difference found between the left and right hands in successful prey capture. The answer seems to be that the requirements of the capture task did not adequately challenge the ballistic reach. A large part of the diet of galagos in their natural habitat is composed of insects, especially flying insects. The advantage of the ballistic reach must be inherent in the rapid movement of the natural prey species. The slowly undulating mealworms placed in the cups of the test apparatus were essentially static targets that rarely resulted in reach errors. Thus, the question of greater left hand efficiency in successful capture must await a different test method, one that challenges the speed of the ballistic reach with the speed of the target.

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